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# Effects of drought legacy and tree species admixing on bacterial growth and respiration in a young forest soil upon drying and rewetting

Md Masudur Rahman[a,*,1], Lettice C. Hicks[b], Kris Verheyen[c], Johannes Rousk[b], Monique Carnol[a]

[a] Laboratory of Plant and Microbial Ecology, InBioS, University of Liège, Botany Bât. 22, Chemin de la Vallée 4, 4000, Liège, Belgium
[b] Section of Microbial Ecology, Department of Biology, Lund University, Ecology Building, 223 62, Lund, Sweden
[c] Forest & Nature Lab, Department of Environment, Ghent University, Geraardsbergsesteenweg 267, B-9090, Gontrode, Belgium

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ABSTRACT

In the context of future climate change, the flush of $CO_2$ emissions from soils after drying-rewetting events could have a strong impact on the terrestrial carbon balance. Mixed forests may be more resistant and resilient to drought events compared to monocultures, and as such may modulate the effects of drought on soil functioning belowground. We investigated the influence of mixed planting and drought legacy on respiration and bacterial growth rates ($^3$H Leucine incorporation) in response to drying-rewetting. Soils were sampled from a 7-year old tree diversity experiment (FORBIO), where oak (*Quercus robur* L.) trees admixed with one or three other tree species were subjected to ~50% precipitation reduction for 2 years ("drought legacy"). Respiration increased immediately after rewetting, whereas bacterial growth only started after a distinct lag phase of ca. 7 h. A legacy of drought reduced bacterial growth and respiration rates upon rewetting, however tree species admixing did not modulate the drought legacy effect. Our results suggest that prolonged decrease in precipitation may lead to a reduced $CO_2$ pulse upon drying-rewetting and admixing up to three tree species with oak in a young afforestation would not alleviate drought legacy effects on bacterial growth and respiration rates.

## 1. Introduction

Climate models have predicted reduced summer precipitation for Europe with more frequent and intense drought and storm events by the end of the century (Kovats et al., 2014), likely increasing the frequency of drying-rewetting events in soils. Rewetting of dry soils typically results in a flush of $CO_2$ emissions to the atmosphere, generally referred to as the 'Birch effect' (Birch, 1958). The balance between soil $CO_2$ emissions through respiration and uptake through photosynthesis is a key to understanding the future role of temperate forests, currently an important carbon sink, in the global carbon budget (Luyssaert et al., 2010). In a mixed forest, it has been shown that soil respiration after a single rain event could lead to the release of up to 10% of the annual net ecosystem production (Lee et al., 2004). In the field, the respiration response of the heterotrophic microbial community upon wetting is likely to be determined by soil moisture before the wetting event, soil drainage condition, substrate type, and storm intensity and duration (Deng et al., 2018; Lee et al., 2004). Further, European forest management is changing from monoculture to mixed species forests, as they are considered to be more resistant and resilient to stress conditions (Isbell et al., 2015; Jactel et al., 2017; Jucker et al., 2014; Pretzsch et al., 2013). Increased tree species diversity, in turn, may both increase soil respiration (Khlifa et al., 2017) and modulate the effects of drought on soil functioning (Rivest et al., 2015). However, the effects of reduced precipitation and tree species diversity upon a drying-rewetting event and the underlying mechanisms are not yet fully understood.

When a soil is subjected to a drying-rewetting event, bacterial growth and respiration rates typically exhibit one of two different response types (Meisner et al., 2013). In a type 1 response, bacterial growth rates increase immediately and linearly from values close to zero upon rewetting (Iovieno and Baath, 2008). This response is associated with high soil respiration rates immediately upon rewetting, followed by an exponential decrease. In a type 2 response, bacterial growth rates increase exponentially after a distinct and extended (up to 20 h) lag phase of near-zero growth, followed by a gradual decrease (Göransson et al., 2013). This response type is associated with high soil respiration immediately after rewetting, which could be sustained for several hours. The actual mechanisms underlying these responses remain elusive and both types of responses can be found in terrestrial ecosystems (Göransson et al., 2013; Meisner et al., 2013). Prolonged

* Corresponding author. Laboratory of Plant and Microbial Ecology, InBioS, University of Liège, Botany Bât. 22, Chemin de la Vallée 4, 4000, Liège, Belgium.
*E-mail addresses:* m.masudur@gmail.com, mmrahman@uliege.be (M.M. Rahman).
[1] Current address: Faculty of agriculture, Sylhet Agricultural University, 3100 Sylhet, Bangladesh.

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drying has been proposed as an explanation for the shift from type 1 to type 2 response pattern within the same soil (Meisner et al., 2017, 2015, 2013). The transition from type 1 to type 2 was ascribed to the low survival of microorganisms in soils dried for a prolonged period of time (Meisner et al., 2015). The previous environmental history may further influence the microbial response upon drying-rewetting. Microbial communities previously exposed to disturbance such as drying-rewetting or freeze-thaw cycles were found to be more resistant to these stresses (Fierer and Schimel, 2002; Stres et al., 2010). Similarly, the amount of precipitation in the past may affect microbial respiration and biomass through changing abiotic conditions and microbial community structure (Evans and Wallenstein, 2012) or via physiological changes (Salazar et al., 2018; Schimel et al., 2007). Moreover, microbial communities exposed to a particular environment may adapt to its condition through changing community levels traits (Evans and Wallenstein, 2014). For example, soils from historically wetter sites were found to be more sensitive to changes in soil moisture than soils from historically drier sites (Hawkes and Keitt, 2015; Hawkes et al., 2017), indicating that the legacy created by previous climatic conditions could play an important role in determining the moisture sensitivity of microorganisms and their responses to rewetting after drought.

Tree species influence soil microbial processes through their influence on soil physico-chemical properties via litter inputs (Carnol and Bazgir, 2013; Thoms et al., 2010; Ushio et al., 2010), changing the microclimate under the canopy (Prescott, 2010), and shifting the microbial community structure (Gunina et al., 2017). Therefore, microbial process rates in mixed species stands may be different to those in monocultures. Photosynthesis and belowground C allocation may be reduced under drought, resulting in lower substrate availability to soil microorganisms (Fuchslueger et al., 2014). Such a negative effect of drought on microorganisms could be alleviated by increasing the tree species diversity or changing tree species composition (Rivest et al., 2015). For example, admixing different tree species with oak offsets the negative impact of drought on soil organic matter decomposition (Rahman et al. in review). Also, the niche complementarity effect (niche partitioning and facilitation) in tree species mixtures has been found to increase under drought (Ratcliffe et al., 2017; Scherer-Lorenzen, 2014), resulting in sustained productivity despite drought conditions (Jucker et al., 2014; Metz et al., 2016; Pretzsch et al., 2013). This suggests that belowground C allocation may be maintained under drought in more diverse forests and soil microorganisms from mixed forests would be less strongly affected by drought compared to monocultures.

In the present study, we used soils from a precipitation reduction experiment (Rahman et al. in review) in a young tree diversity experiment (Verheyen et al., 2013). We investigated the effects of drought legacy and different tree species admixture levels (oak monoculture, or oak admixed with one or three other tree species) on the type of bacterial growth and respiration responses to rewetting dry soils. We hypothesized that i) soils with a legacy of drought would exhibit different types of bacterial growth and respiration patterns upon drying-rewetting by shifting from type 1 to type 2 response, ii) the drought legacy may reduce the bacterial growth and respiration rates upon drying-rewetting, and iii) the drought legacy effect might be weakened by a higher number of tree species, and, therefore, we would observe a more pronounced drought legacy effect in monocultures than in the mixed stands.

## 2. Materials and methods

### 2.1. Soils and field treatment

Soils were sampled from the Zedelgem site of the FORBIO experiment in Belgium (Verheyen et al., 2013), belonging to the worldwide Tree Diversity Network (http://www.treedivnet.ugent.be/,Verheyen et al., 2016). The site is close to the North Sea (51°9′ N 3°7′ E), with a mean annual precipitation of 855 mm and an average temperature of 10.5 °C (1981–2010; RMI, Royal Meteorological Institute, Belgium, https://www.meteo.be/en). Soils have been classified as relatively dry sandy soil (Podzol) to moderately wet loamy sand (gleysol) (Verheyen et al., 2013). The site was previously agricultural land and was planted with five locally adapted tree species (*Betula pendula* Roth, *Fagus sylvatica* L., *Quercus robur* L., *Tilia cordata* Mill., and *Pinus sylvestris* L.) in winter 2009–2010. In the FORBIO experiment, tree species richness levels varied from monocultures to four-species mixtures. In two-to four-species mixtures, trees were planted in small monoculture blocks of 3 × 3 trees with a distance of 1.5 m between the trees. The understorey vegetation was inventoried following the experiment establishment in 2011, showing that the community was typical for a rich, moist grassland in central Europe (Verheyen et al., 2013). The understorey was cut annually during the first 3 years after planting, but was since left unmanaged. During the drought experiment, the vegetation remained similar to that determined in initial surveys, and no encroachment of woody shrubs or trees was found (personal observation, MM Rahman). As such, the plant community in the plots of the experiment is determined by the planted tree composition along with the grass-dominated understorey associated with the trees.

A precipitation reduction (hereafter drought) experiment was started in April 2015 to assess the performance of oak and beech saplings under drought conditions. Three drought and three control plots of 3 m × 3 m were established around oak and beech trees, surrounded each by the same species and one to three other tree species (species admixture level), within the FORBIO experiment (Rahman et al. in review). The tree species admixture levels thus represented a dilution gradient from monoculture to admixture of one to three site-adapted tree species with oak or beech. The tree species composition of the replicate plots for two, three and four tree species plots was different (Table S1, Supplementary information). Precipitation was reduced by installing a rainout shelter made of PVC gutters (~12 cm wide) placed at an interval of ~25 cm (Rahman et al. in review). The gutters were placed at a height of 0.95 m from the ground at the upper side and 0.75 m from the ground in the lower side to promote faster drainage. A 6 m long gutter was placed at the lower side to channel the intercepted precipitation away from the plot. The amount of precipitation reduction was assessed over 44 days in summer 2016 by placing a rainfall collector under and outside the rainout shelter in monoculture, two- and three -species plots. The gutters covered approximately 50% of the plot and intercepted about 45–55% of the total precipitation. Any litter that had been intercepted by the shelter was removed and placed under the shelter. However, few leaves were caught in the gutters, and as the plots were in the middle of the forest and surrounded by dense canopy it was unlikely that leaves were blown off the shelter, hence the potential for litter loss as a result of the shelter was considered as negligible. In addition to rainout shelters in drought plots, three rainout shelters with reverse gutters (no precipitation interception) were also installed to assess the shading effect. Mean soil temperatures during the day at 5 cm depth from April 2016 to March 2017 were 10.6 ± 0.25 °C in the control, 10.5 ± 0.24 °C in the drought and 10.5 ± 0.24 °C in the reverse gutter plots, confirming that there was no substantial shading effect due to the rainout shelter. The volumetric soil water content (0–30 cm) over the 22 months prior to soil sampling was about 15% less in drought plots compared to ambient plots (Fig. S1; supplementary information).

### 2.2. Soil sampling and chemical analysis

In this study, soils were sampled from oak plots only. Among the four tree species admixture levels, soils were sampled from one (oak monocultures), two (1 species admixed to oak) and four (3 species admixed to oak) species admixture plots. Soils were sampled in May 2017, two years after the beginning of drought experiment from the ambient (hereafter 'ambient control') and drought (hereafter 'drought

legacy') plots. In each plot, four soil cores were taken using a plastic corer (7 cm diameter) halfway between the central oak tree and four corner trees (ca. 1 m). Soils were transported to the laboratory in a sealed double zip lock bag and stored at room temperature. After removing the litter layer, the top 5 cm soils were retained for analysis and experimentation. Soils from the four cores from each plot were mixed together to form one composite sample per plot. Soils were sieved (4 mm) to remove plant, root material and other debris. The soils used by both Hicks et al. (2018) and in this study were sampled together.

Soil subsamples were used to measure soil moisture (105 °C, until constant mass). Soil organic matter (SOM) content was measured as loss on ignition through burning the dry soils in a muffle oven at 600 °C for 12 h. Soil C and N content was determined in a vario MICRO cube elemental analyser (Elementar Analysensysteme GmbH, Hanau, Germany). Soil water holding capacity (WHC) was measured by placing 5 g soil in a 50 ml plastic tube, with the bottom covered with fine nylon mesh (50 µm). The top of the tube was covered with parafilm and the tube was dipped in water for 24 h before draining the excess water for 6 h. The WHC of the soil was calculated from the amount of water absorbed by the soil and the moisture content of the soil, and expressed as % dry weight basis. Soil pH ($H_2O$) was measured in a 1:5 (w/v) soil: $H_2O$ solution using a pH meter. The electrical conductivity (EC) was measured in the same solution using an EC meter.

### 2.3. Drying-rewetting experiments and measurements

Soils from both ambient control and drought legacy plots were first adjusted to 50% WHC, by adding demineralized water and kept at room temperature overnight before storage at 4 °C (2–10 days before drying-rewetting). These adjustments from field moist conditions were sufficiently small (Table S2, supplementary information) to not induce pronounced drying-rewetting dynamics and thus to stabilise within a few hours after adjustment (Meisner et al., 2017). Soil subsamples at 50% WHC and were kept at 4 °C when not used for measurements, acting as 'moist control'. Soils were stored at low temperatures to better reflect the freshly sampled soils, and to minimise the storage effect since sampling, which can affect the response type to drying-rewetting (Meisner et al., 2015). Both bacterial growth and respiration rates (see below) of the moist control soils were measured once per day along with the dried-rewetted soils during the week of the experiment.

For the drying-rewetting experiment, subsamples of soils from all field treatments were air-dried under a fan at room temperature for 2 days. The air-drying treatment reduced soil moisture content to a similar in all soils, reaching stable conditions at ca. 3.3% WHC (Table S2, supplementary information). The soils were then rewetted to 50% WHC and incubated at 17 °C for one week; a temperature close to the mean summer soil temperature for the site (Hicks et al., 2018). Bacterial growth was measured at 16 time points after rewetting (0, 3, 6, 9, 15, 21, 27, 33, 42, 48, 57, 72, 96, 120, 144 and 168 h). Bacterial growth rates were estimated by measuring the rate of $^3$H-Leucine (Leu) incorporation into a suspension of microbial cells, extracted from the soil using the homogenization/centrifugation technique (Bååth et al., 2001; Rousk and Bååth, 2011). At each sampling time, 1 g soil was mixed with 20 ml demineralized water in a 50 ml tube. The suspension was vortexed for 3 min and centrifuged at 3000 rpm for 10 min before 1.5 ml of supernatant was sampled. Leucine incorporation rate was measured in this extract by adding 2 µl 1-[4,5-3H]-Leucine (5.7 TBq mmol$^{-1}$, Perkin Elmer, USA) and unlabelled Leu with a final concentration of 275 nM Leu in the bacterial suspension. After 1 h incubation at 17 °C, bacterial growth was terminated by adding 100% TCA and the samples were washed as described by Bååth et al. (2001). The radioactivity, as DPM (disintegration per minute), was measured after adding 1 ml scintillation cocktail in a liquid scintillator counter (Perkin Elmer, USA). The amount of leucine incorporated into extracted bacteria (pmol Leu g$^{-1}$ soil h$^{-1}$) was used as a measure of bacterial growth (Rousk and Bååth, 2011).

Soil respiration was measured over 11 time intervals after rewetting (0–6, 6–12, 12–18, 18–24, 24–30, 36–42, 48–54, 72–84, 96–120, 120–144 and 144–168 h). The headspace of a glass vial containing 1 g soil was first purged with pressurized air, before vials were sealed and incubated at 17 °C for 6, 12 or 24 h (as specified for the specific time-points, above). Due to rapid changes in respiration rates at the beginning of the incubation, the sampling frequency was designed to match this dynamic. As respiration rates decreased over time, incubation times were increased to accumulate similar concentrations of $CO_2$ in the headspace of the vials, to ensure similar measurement precision throughout the study period. The amount of $CO_2$ produced during the incubation was determined using a gas chromatograph equipped with a methanizer and flame ionization detector (6500GC System, YL instrument, South Korea). The result was expressed as µg $CO_2$ g soil$^{-1}$ h$^{-1}$.

### 2.4. Data analysis

The duration of the lag phase with a bacterial growth rate near zero was estimated using a modified Gompertz equation (Zwietering et al., 1990), as described by Meisner et al. (2017). Cumulative respiration and bacterial growth rates after rewetting were calculated as the sum of products of values and time intervals. For respiration rates, midpoints between the pairs of time periods were used in the calculations. Cumulative bacterial growth was calculated at 57 h after rewetting, when maximum rates were attained i.e. when rates switched from increasing to decreasing, likely due to substrate availability limiting bacterial growth. Similarly, cumulative respiration rates were calculated at 54 h after rewetting. The ratio of cumulative respiration to bacterial growth was also calculated for these time points, and considered as a proxy of microbial carbon use efficiency. Cumulative values and ratios were also calculated for the whole duration of the experiment (168 h). We used linear mixed effect models ('lmer' function of 'lme4' package) (Bates et al., 2015) to test the effects of tree species admixture and drought legacy on the response variables (lag phase, bacterial growth and respiration in moist control soils, and cumulative bacterial growth and respiration at 57 and 168 h after rewetting). Tree species admixture and drought legacy were used as fixed effects while 'plot', accounting for different species composition of the plots, was used as random effect in the model. The model calculates the F and p values using Satterthwaite approximation for degrees of freedom (Kuznetsova et al., 2016).

Effects of tree species admixture and drought legacy on bacterial growth and respiration rates were tested on both actual and normalized (values at each time point/period divided by the average growth and respiration rate of the moist control soils) values. Due to the repeated measures design, data were analysed with linear mixed effects models, accounting for the dependency of different measurements through time on the same sample. Treatment (drought legacy, ambient control), tree species admixture (1, 2 and 4) and time were defined as fixed effects and the individual samples were used as random effects. Analyses were performed using the 'lme' function of the 'nlme' package (Pinheiro et al., 2014) where we used 'corCAR1' function to account for the autocorrelation between time points for each sample. The overall effects of tree species admixture and drought legacy were assessed by the 'anova' analysis of the model. If a significant effect was found, Tukey HSD post-hoc test was performed to compare the means between the treatments using the 'multcomp' package (Hothorn et al., 2008). Normality of the residuals was tested using the Shapiro-Wilk test and diagnostic residuals plots. Data were log transformed if there was an obvious deviation from the normality assumption. All analyses were performed using RStudio, version 1.1.383 (R Core Team, 2014).

## 3. Results

### 3.1. Soil properties

Soil organic matter content ranged from 3.6 to 4.1% with no effect

**Table 1**
Soil chemical properties, bacterial growth, respiration rates in the moist control soils, and lag phase for bacterial growth after drying-rewetting. 1, 2 and 4 species indicate oak monocultures and admixture of 1 or 3 tree species to oak, respectively. Values are means ± SE, n = 3. Only bacterial growth rates were significantly ($p<0.01$) higher in the ambient control (AC) than in the drought legacy (DL) plots, without any effect of tree species admixture.

| | 1 species | | 2 species | | 4 species | |
|---|---|---|---|---|---|---|
| | AC | DL | AC | DL | AC | DL |
| SOM (%) | 3.75 ± 0.37 | 3.58 ± 0.31 | 4.06 ± 0.36 | 3.76 ± 0.12 | 3.81 ± 0.26 | 3.77 ± 0.30 |
| pH ($H_2O$) | 6.27 ± 0.1 | 6.17 ± 0.04 | 6.10 ± 0.06 | 5.90 ± 0.08 | 6.20 ± 0.06 | 6.17 ± 0.16 |
| EC (μS/cm) | 33.13 ± 3.0 | 33.90 ± 1.04 | 31.50 ± 2.84 | 33.13 ± 1.94 | 32.90 ± 2.3 | 34.70 ± 1.5 |
| C (%) | 1.67 ± 0.33 | 1.82 ± 0.3 | 1.50 ± 0.16 | 1.60 ± 0.28 | 1.81 ± 0.24 | 1.76 ± 0.05 |
| N (%) | 0.12 ± 0.02 | 0.14 ± 0.02 | 0.12 ± 0.01 | 0.12 ± 0.02 | 0.16 ± 0.02 | 0.15 ± 0.006 |
| Average bacterial growth in moist control soil (pmol Leu. $g^{-1}$ soil $h^{-1}$) | 10.23 ± 0.60 | 6.80 ± 0.34 | 8.28 ± 0.34 | 6.93 ± 0.50 | 7.92 ± 0.37 | 6.46 ± 0.35 |
| Average respiration in moist control soil (μg $CO_2$ $g^{-1}$ soil $h^{-1}$) | 1.59 ± 0.13 | 1.19 ± 0.12 | 1.53 ± 0.11 | 1.61 ± 0.14 | 1.60 ± 0.11 | 1.17 ± 0.09 |
| Lag phase (h) | 4.95 ± 0.51 | 6.60 ± 2.06 | 8.07 ± 1.12 | 8.59 ± 1.59 | 6.97 ± 2.29 | 6.83 ± 1.51 |

of drought legacy and tree species admixture (Table 1). Soil pH ranged between 5.9 and 6.3 with no significant difference between the drought treatments and tree species admixture levels. The electrical conductivity, C and N contents of the soil did not vary between the drought treatments and tree species admixture levels (Table 1).

### 3.2. Bacterial growth and respiration rates in moist control soils

Bacterial growth and respiration rates of moist control followed a similar dynamic over time, as they did not change significantly during the week of incubation and were not influenced by tree species admixture (Table 1). Average bacterial growth rates across all tree species admixture levels was higher ($p<0.01$) in soils from ambient control plots (8.8 ± 0.4 pmol Leu $g^{-1}$ soil $h^{-1}$) compared to soils from drought legacy plots (6.7 ± 0.4 pmol Leu $g^{-1}$ soil $h^{-1}$) (Table 1). Drought legacy and tree species admixture levels had no significant effect on soil respiration rates of the moist control soils (Table 1).

### 3.3. Bacterial growth rates after drying-rewetting

Bacterial growth rates exhibited a similar pattern in all treatments during the week of incubation following drying-rewetting (Fig. 1). A lag phase of 5.0–8.6 h was observed before the onset of bacterial growth, with no significant difference between the treatments (Table 1). After the lag phase, growth rates increased exponentially until ca. 50 h after rewetting (Fig. 1). Thereafter, growth rates decreased and stabilized after 96 h, resulting in large differences between time points during the study period (Table 2). Bacterial growth rates after rewetting were significantly lower in drought legacy treatments, without any effect of tree species admixture (Table 2).

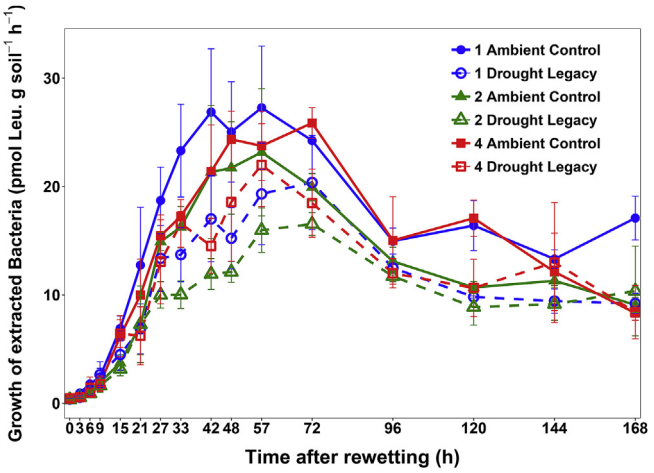


**Fig. 1.** Mean bacterial growth rates after drying-rewetting of soils previously exposed to 50% precipitation reduction in the field for 2 years (drought legacy, dashed lines) and ambient control (solid lines). 1, 2 and 4 in the legend indicate oak monocultures and admixture of 1 or 3 tree species to oak, respectively. Error bars are SEM, n = 3.

**Table 2**
ANOVA table from repeated measures mixed effects models for bacterial growth rates (pmol Leu. $g^{-1}$ soil $h^{-1}$) and respiration rates (μg $CO_2$ $g^{-1}$ soil $h^{-1}$) of dried-rewetted soils measured over time. Admixture levels represent oak monocultures and admixture of 1 or 3 tree species to oak. Drought legacy indicates soils previously exposed to 50% precipitation reduction in the field for 2 years. Time represents different times of measurement during 7 days after drying-rewetting. Bold indicates p was close or lower than 0.05.

| Sources of variation | Numerator df | Denumerator df | F-value | p value |
|---|---|---|---|---|
| **Bacterial growth rates**[a] | | | | |
| Intercept | 1 | 210 | 1372.50 | < **0.01** |
| Admixture (A) | 2 | 14 | 1.80 | 0.15 |
| Drought legacy (D) | 1 | 14 | 6.22 | **0.03** |
| Time (T) | 15 | 210 | 201.88 | < **0.01** |
| A × T | 30 | 210 | 0.53 | 0.97 |
| D × T | 15 | 210 | 0.69 | 0.79 |
| **Respiration rates** | | | | |
| Intercept | 1 | 140 | 552.80 | < **0.01** |
| Admixture (A) | 2 | 2 | 1.80 | 0.12 |
| Drought legacy (D) | 1 | 2 | 3.99 | **0.06** |
| Time (T) | 10 | 140 | 73.41 | < **0.01** |
| A × T | 20 | 140 | 1.80 | **0.02** |
| D × T | 10 | 140 | 1.27 | 0.25 |

[a] Data were log transformed.

When the growth rates were normalized to moist control soils, there was no drought legacy effect, but a marginally significant effect of tree species admixture was observed (Table S3, Fig. S2, Supplementary information). Post-hoc analysis showed that bacterial growth rates were higher (marginally significant; p = 0.08) in four-species plots compared to monoculture plots.

Cumulative bacterial growth after 57 h of drying-rewetting was significantly lower in soils with drought legacy compared to ambient control soils (Fig. 2a, Table 3). Tree species admixture levels did not significantly influence cumulative bacterial growth (Table 3). Cumulative values calculated over the whole duration of the experiment (168 h) and statistics (leading to the same conclusions) can be found in the supplementary information (Fig. S3a, S5; Table S4).

### 3.4. Respiration rates after drying-rewetting

The pattern of respiration rates during a week following drying-rewetting was similar in all soils (Fig. 3). During the incubation period, respiration rates were high immediately after rewetting, followed by a decrease, and stabilization at 96–120 h after rewetting (Fig. 3). The respiration rates differed significantly between time points and there was a significant interaction between the time points and tree species admixture level (Table 2). Rates following rewetting were higher

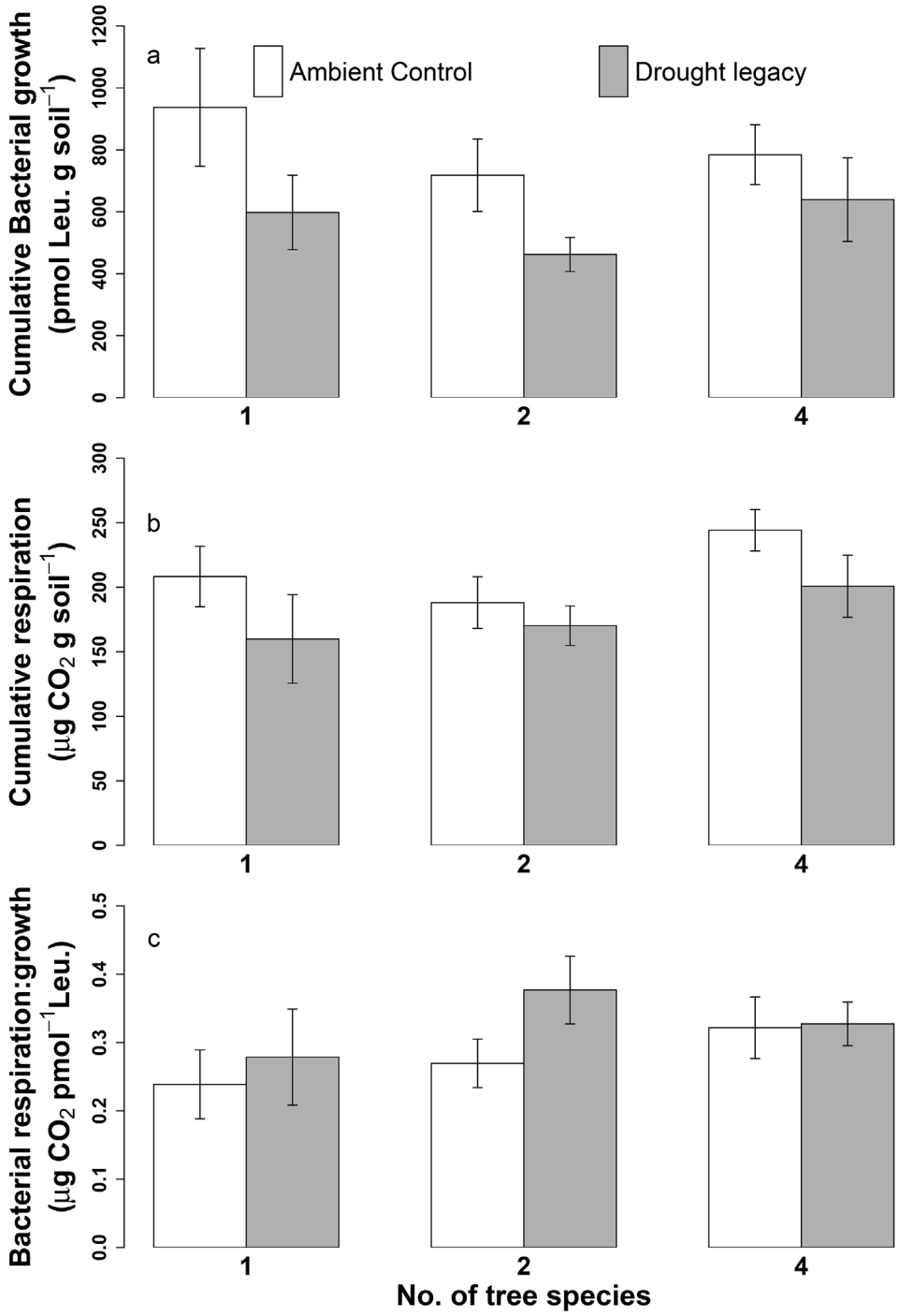


**Fig. 2.** (a) Cumulative bacterial growth, (b) cumulative respiration and (c) cumulative respiration: growth ratio in soils previously exposed to 50% precipitation reduction in the field for 2 years (drought legacy) and ambient control at 57 h and 54 h after drying-rewetting. 1, 2 and 4 indicate oak monocultures and admixture of 1 or 3 tree species to oak. Error bars are SEM, n = 3.

(marginally significant, p = 0.06) in ambient control plots but did not differ significantly between tree species admixture levels (Table 2). There was no drought legacy and tree species admixing effect on respiration rates when values were normalized to moist controls soils (Table S3, Fig. S4, Supplementary information).

Drought legacy reduced (marginally significant: p = 0.07) the cumulative respiration at 54 h after drying-rewetting, without any effect of tree species admixture (Fig. 2b, Table 3). The respiration to growth ratio did not differ significantly between the drought treatment and between the tree species admixture levels (Fig. 2c, Table 3). Cumulative values calculated over the whole duration of the experiment (168 h) and statistics (leading to the same conclusions) can be found in the supplementary information (Fig. S3b-c, S5; Table S4).

## 4. Discussion

### *4.1. Drought legacy does not change the type of bacterial growth and respiration responses to rewetting*

We expected that a legacy of drought would result in different bacterial growth and respiration patterns upon drying-rewetting of soils. In contrast, we observed similar “type 2” response patterns

**Table 3**
ANOVA table from mixed effects models for cumulative growth (pmol Leu. $g^{-1}$ soil), respiration (μg $CO_2$ $g^{-1}$ soil), and respiration: growth ratios in dried-rewetted soils after 57 h and 54 h, respectively. Admixture levels represent oak monocultures and admixture of 1 or 3 tree species to oak. Drought legacy indicates soils previously exposed to 50% precipitation reduction in the field for 2 years. Bold indicates p was close or lower than 0.05.

| Sources of variation | Numerator df | Denumerator df | Mean Sq. | F-value | p value |
|---|---|---|---|---|---|
| **Cumulative bacterial growth after 57 h** | | | | | |
| Admixture (A) | 2 | 8.11 | 47437 | 1.00 | 0.26 |
| Drought legacy (D) | 1 | 8.11 | 273616 | 5.77 | **0.04** |
| A × D | 2 | 8.11 | 14232 | 0.30 | 0.74 |
| **Cumulative respiration after 54 h** | | | | | |
| Admixture (A) | 2 | 12 | 3376 | 2.11 | 0.16 |
| Drought legacy (D) | 1 | 12 | 6010 | 3.76 | **0.07** |
| A × D | 2 | 12 | 403 | 0.25 | 0.78 |
| **Cumulative respiration: bacterial growth** | | | | | |
| Admixture (A) | 2 | 9 | 0.004 | 0.71 | 0.33 |
| Drought legacy (D) | 1 | 9 | 0.011 | 1.77 | 0.22 |
| A × D | 2 | 9 | 0.004 | 0.61 | 0.56 |

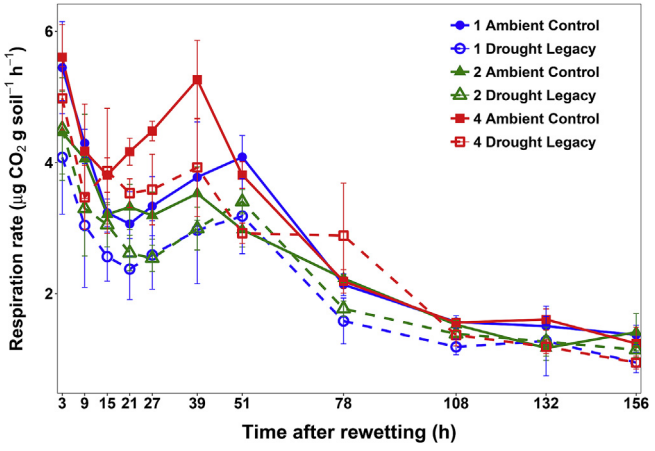


**Fig. 3.** Mean respiration rates after drying-rewetting in soils previously exposed to 50% precipitation reduction in the field for 2 years (drought legacy, dashed lines) and ambient control (solid lines). 1, 2 and 4 in the legend indicate oak monocultures and admixture of 1 or 3 tree species to oak. Time shown in the x-axis are the midpoints of the measurement periods. Error bars are SEM, n = 3.

(Meisner et al., 2015) of bacterial growth and respiration rates (Göransson et al., 2013) for soils from both drought legacy (50% precipitation reduction for 2 years in the field) and ambient control soils, and from all tree species admixture levels. Previous laboratory studies have observed a shift from a type 1 to a type 2 response with increasing duration (Meisner et al., 2015, 2013) and intensity (Meisner et al., 2017; Rath et al., 2017) of drying immediately prior to rewetting, and a shift from a type 2 to a type 1 response with partial drying before rewetting (Meisner et al., 2017). From these previous observations, the shift in the type of response may be attributed to the responses of microorganisms to drying (survival/community structure), with a 'harsh' drying leading to lower microbial biomass, more damaged cells, a lower ratio of active to inactive microorganisms in soil (Barnard et al., 2015, 2013; Heděnec et al., 2018; Placella et al., 2012; Salazar et al., 2018), and a type 2 growth-response. Other studies have shown that a history of drought might lead to an adaptation of the microbial community, to one which is less sensitive to changes in soil moisture (Hawkes and Keitt, 2015; Thion and Prosser, 2014). However, in our study, drought legacy soils exhibited the same type 2 response as ambient control soils. There was also no significant difference in the lag phase before the onset of bacterial growth between treatments. All this suggests that, despite a history of drought, the drying perturbation in the laboratory was experienced as equally harsh by microorganisms in drought exposed and ambient control soils, and that communities had not grown adapted to the perturbations in the drought legacy soils.

### 4.2. Drought legacy reduces bacterial growth and respiration rates

As expected, a legacy of drought induced lower bacterial growth rates and marginally significant lower soil respiration rates upon drying-rewetting. A drought legacy effect, reducing soil respiration upon drying-rewetting, has also been reported in other forest (Göransson et al., 2013) and grassland studies (Evans and Wallenstein, 2012; Hawkes et al., 2017). Lower C availability in drought-exposed soils may explain this response, as drought typically reduces plant productivity and belowground C allocation (Fuchslueger et al., 2014; Zang et al., 2014), leading to reduced microbial process rates. A drought legacy effect leading to lower bacterial growth and respiration under stable moisture and temperature conditions, along with reduced microbial biomass, was observed in these same soils (Hicks et al., 2018). Thus, a lower availability of labile C in drought-exposed soils might account for both lower biomass and lower process rates. Indeed, although rates of growth and respiration following rewetting here were lower in drought-exposed soils compared to ambient controls, once normalized to rates in moist control soils, these differences disappeared. Also, using the ratio of bacterial growth to respiration as an index for the microbial carbon-use efficiency, it was found to be similar over the 7-day incubation between the drought legacy and ambient control soils. This suggests that the microbial sensitivity to the drying-rewetting event was similar for both treatments, and the drought-legacy effect instead manifested because of lower process rates, which were also reflected in moist control soils under stable conditions.

### 4.3. Tree species admixing does not modulate drought legacy effects on bacterial growth and respiration responses to rewetting

Belowground microbial communities are intimately linked to aboveground plant communities (Gunina et al., 2017; Scheibe et al., 2015; Thoms et al., 2010), which determine the C input to soil from litterfall, roots and root exudates. Mixed forests generally function with higher stability than monocultures under disturbances, such as drought stress, due to the effects of niche complementarity (Grossiord et al., 2014; Kreyling et al., 2017; Mina et al., 2018; Morin et al., 2011; Ratcliffe et al., 2017). We therefore expected stronger drought legacy effects on microbial growth and respiration rates in monocultures compared to two- and four-species admixture plots. We did not observe a significant effect of tree species admixture on absolute rates of bacterial growth and respiration after rewetting or on cumulative bacterial growth and respiration over the incubation period. However, after normalization to rates in the moist control soils, bacterial growth was higher in soils from four-species admixture plots compared to soils from oak monocultures and two-species admixtures. This finding may indicate a potential effect of tree species composition (Brunel et al., 2017) on soil bacterial growth responses following drying-rewetting, possibly driven by the presence of pine or lime trees in the four-species admixture. Also, the higher functional diversity of plants in the four-species mixtures could have resulted in greater resource exploitation (Forrester and Bauhus, 2016; Hooper et al., 2005; Metz et al., 2016), leading to higher C and nutrient availability to soil microorganisms, thus supporting the higher bacterial growth following rewetting. This finding is also consistent with microbial growth rates and bacterial community composition measured in the same soils under stable temperature and moisture conditions to capture stable state rates, which were disproportionately affected by a legacy of drought in soils under oak monocultures compared to three- and four-species admixture plots (Hicks et al., 2018). Together, these observations suggest that admixing

oak with the tree species included here might lead to higher bacterial growth rates after drying-rewetting.

## 5. Conclusion

We investigated whether tree species admixing could moderate the legacy effects of drought on bacterial growth and respiration rates following soil drying-rewetting. We found that in a young plantation, a legacy of drought (2 years of 50% precipitation reduction) reduced bacterial growth and respiration rates upon rewetting, but that tree species admixing did not modulate these responses. Bacterial growth rates normalized to rates in moist control soils, however, suggested that admixing oak with three other tree species would support higher bacterial growth following soil drying-rewetting. Overall, our findings indicate that prolonged reduction of precipitation in central European forests might lead to a reduced $CO_2$ pulse following drying-rewetting events and thus a reduced loss of C from soils.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2018.09.026.

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